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ACKNOWLEDGMENT. The work is partly sponsored by University Malaya UMRG

Grant no. RG263/13AFR and UM/MOHE High Impact Research Grant (UMC/HIR/MOHE/SC/27). The samples for this study are taken from core sample of Archeological research of Bukit Bunuh, Peninsular Malaysia: Grant no. 1002/Parkeo/910202DE2012 headed by Prof. Mokhtar Saidin from University Sains Malaysia. Dr Zuhar Zahir is thanked for providing the granite samples. Field work for this project is partly sponsored by PPP grant from University Malaya (PV087-2012A). Armstrong Hilton Limited is acknowledged for editing the English.

Received 3 December 2014; revised accepted 21 April 2015

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Species diversity–primary productivity relationships in a nitrogen amendment experiment in grasslands at Varanasi, India

The accelerated loss of biodiversity due to the land use and global climate changes has proved detrimental to ecosystem functioning (i.e. litter decomposition, nutrient cycling, energy storage and flux, ecosystem services, etc.). It has attracted intensive experiments during the past four decades, because primary productivity (P) as a measure of ecosystem functioning may or may not be closely coupled with species diversity (D)^{1–7}. Nevertheless, relationships between the above have been attributed to changes in the size and composition of competitive plant functional groups under varied resource availability and diverse ecological incidents⁷.

Several experimental and theoretical studies have led to vital debates on *D–P* relationships^{6–9}. The reviews by Waide *et al.*¹⁰ and Mittelbach *et al.*¹¹ showed variations in the shape of *D–P* relationships, depending on the study systems, spatial scales, environmental factors and competitive ability of species, and functional group compositions⁷. Positive *D–P* relationship was reported in many studies^{3,12–14}. Nutrient input studies have suggested higher productivity with lower species diversity^{9,15,16}. On the other hand, some biodiversity experiments showed a reduction in species diversity due to decline in productivity^{4–8}. Several other trends have been suggested, including none⁶ or idiosyncratic relationships between species diversity and primary productivity¹⁷. Many studies, using cor-

relations across different sites or nutrient additions, suggested a hump-shaped curve for the relationship between diversity and productivity (see refs 10, 11 for details). Grime¹ was the first to note a hump-shaped relationship between diversity and productivity. Majority of the studies, including meta analysis suggested that unimodal *D–P* relationship is more prevalent in natural communities¹⁸, while others suggested that a monotonic positive and linear relationship is more common^{4,19,20}. Hence, the relationship between plant diversity and primary productivity has continued to be an essential issue in ecological and environmental sciences^{3–9}.

In view of the aforesaid debate, the present study was conducted to answer the following questions: (i) Does species diversity exhibit a linear relationship with primary productivity? (ii) Does plant functional group composition determine the *D–P* relationships in nitrogen (N)-amended experimental plots located in a dry tropical environment of India?

The study was based on three doses of N-amendment (control, 6 and 12 g N m⁻² year⁻¹) experienced by the herbaceous grassland vegetation from January 2007 to December 2010. The doses 6 g and 12 g N are referred to as low and high N treatments respectively. In this study we used 6 and 12 g N m⁻² year⁻¹ because in our previous study the application of 6 g N m⁻² year⁻¹ did not saturate the soil. In this experiment, a total of 135,

1 × 1 m plots (15 locations × 3 treatments × 3 replicates), all situated on plain, alluvial grounds within the campus of the Banaras Hindu University (BHU), Varanasi, India (24°18'N and 83°03'E and 76 m amsl) were used. The soil is moderately fertile being low in soil-C (0.84 ± 0.07%) and soil-N (0.08 ± 0.01%). The soil pH is neutral to alkaline (7.19 ± 0.12). Data were collected in the year 2011. Species diversity was calculated using Shannon–Wiener equation²¹. The number of species/m² was used for computing the species richness²². Sheldon²³ equation was used to quantify the evenness. Aboveground peak herbaceous biomass was considered as a measure of primary productivity^{6,24,25}. These parameters were determined for each N level in each season. Contribution of diverse species to total plant biomass was assessed by species separation in June, September, December and March which corresponded respectively, with the start of vigorous growth of herbaceous vegetation at the beginning of the rainy season, the time when rainy-season vegetation is at its best, the mid-winter phase of relative inactivity, and the period when flowering and fruiting of the plants during the summer season show renewed but limited growth²⁴. The average values of the three growing seasons were used to establish the *D–P* relationships using SPSS statistical software.

The number of species, relative biomass and functional groups represented

Table 1. Mean herbaceous species for various trait categories in different levels of nitrogen treatment at experimental plots of Banaras Hindu University, Varanasi

Trait	Trait category	Control	6 g N m ⁻² year ⁻¹	12 g N m ⁻² year ⁻¹
Growth forms	Forbs	6.05 (0.40)	9.40 (0.34)	5.42 (0.34)
	Grasses	3.73 (0.07)	7.27 (0.09)	6.23 (0.13)
	Legumes	1.22 (0.05)	0.83 (0.02)	0.35 (0.02)
Height	Short	4.24 (0.26)	6.87 (0.20)	2.41 (0.15)
	Medium	1.77 (0.13)	2.37 (0.10)	1.06 (0.09)
	Long	4.99 (0.40)	8.26 (0.45)	8.53 (0.54)
Nitrogen-fixing symbiont	N-fixers	2.83 (0.05)	2.11 (0.03)	0.74 (0.02)
	Non N-fixers	8.17 (0.50)	15.39 (0.53)	11.25 (0.57)
Total species number		30	49	32
Rare species number (m ⁻²)		5	6	2
Total biomass (g m ⁻²)		27.60	33.10	35.90

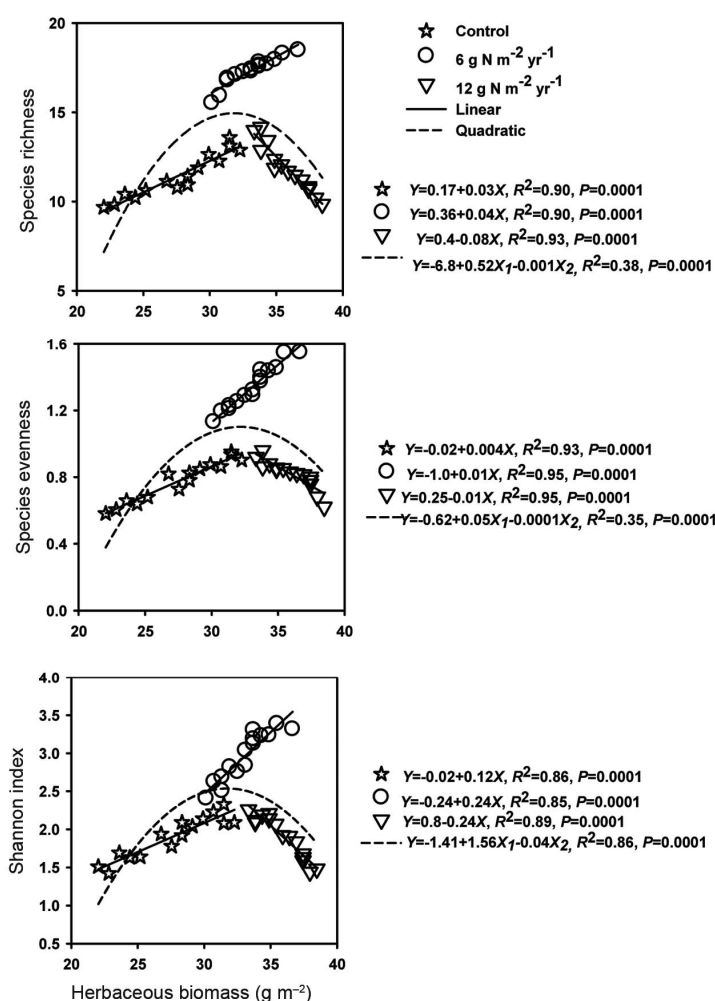


Figure 1. Relationship between herbaceous species diversity and primary productivity in different nitrogen enrichment levels at the Banaras Hindu University, Varanasi.

by each species at the experimental plots are presented in Appendix (Table A1). The experimental plots harboured 49 species, 42 genera and 24 families. Thirty-nine per cent species were common to the control, low and high N-treated plots, and 27% species occurred only at N (6 and 12 g N m⁻² year⁻¹) treated plots. Six species were restricted to 6 g N-treated plots only (Appendix, Table A1).

Figure 1 shows that for each N level, species richness, evenness and Shannon index are linearly and significantly related with primary productivity. The nature of relationships for control and low N-treatment plots was positive, while for high N-treatment plots, the relationships were negative. When the *D-P* relationships were established using pooled data of the entire plots (control and N-treated plots), the species richness, evenness and Shannon–Wiener indices showed quadratic responses against primary productivity. Thus, the study shows three patterns for *D-P* relationships: (i) positive, when the system experiences either no or relatively low N input at 15 m² area; (ii) negative, when the system experiences comparatively high N input in the same area, and (iii) unimodal, when the system experiences differences in N treatment at relatively larger area (45 m²). The existence of positive *D-P* relationships in control as well as in low N-treated plots, may suggest that under zero external N input the natural ecosystem processes just

maintained productivity and species diversity, but as soon as N ($6 \text{ g m}^{-2} \text{ year}^{-1}$) was added to the system it facilitated the germination and establishment of existing dominant, common, rare as well as other nitrophilic species (Table 1). Due to these events, both the species number

and their biomass buildup increased (Table 1) and yielded a positive $D-P$ relationship²⁵. In the next situation, when a comparatively higher amount of N (12 g) was added to the system, certain highly aggressive/nitrophilic and tall-statured functional groups dominated the

system by accumulating biomass and they excluded/suppressed the N-sensitive (N-fixers and legumes), short-statured and rare species (Table 1) from the system; therefore, a negative $D-P$ relationship occurred¹⁵. Thus, the competition for light and nutrients was the possible mechanism in modulating the negative $D-P$ relationship²⁶ at relatively higher N input. The above two types of relationships occasioned by changes in species composition brought about by differences in N-availability at small spatial scale, caused the occurrence of unimodal $D-P$ relationship at the larger spatial scale (pooling of all 45, $1 \times 1 \text{ m}$ plots; thus, total number of observations was 45 and area covered was 45 m^2). It can be argued that progressive loss of species and gain in productivity over the study period with N-addition (6 or $12 \text{ g N m}^{-2} \text{ year}^{-1}$) changed the community composition²⁷, such that an unimodal $D-P$ relationship was realized.

Moreover, the inverse relationship between diversity and productivity in 12 g N -treated plots corroborates the dynamic equilibrium hypothesis of Huston⁷, because the interacting functional group compositions were unequally affected by N-enrichment, and the system was deliberately destabilized due to elimination of competitively inferior plant functional groups. The high productivity in this condition may be because of high growth rates of superior plant functional groups²⁸. Interestingly, the high diversity in 6 g N -treated plots may be attributed to the less competition among the composition of competing functional groups²⁹⁻³¹. Based on these explanations, the $D-P$ relationship appears to be driven by the plant functional group composition.

The occurrences of the above three patterns in three different conditions were similar to the findings of Connell and Orias¹², Pianka *et al.*¹³, Loreau *et al.*⁵ and Huston¹⁴, where diversity was positively related with productivity; Reich and Hobbie⁹, Stevens *et al.*¹⁵, Clark and Tilman¹⁶ and Grime³² for negative relationship between $D-P$, and Grime¹ for unimodal relationship. Contrary to the present report, Adler *et al.*⁶ found no relationship between species richness and primary productivity. Moreover, the present study was unable to compare with the results of Isbell *et al.*⁴ and Tilman *et al.*⁸ due to constraints in temporal data.

Appendix. Table A1. Number of herbaceous species with their families and biomass at experimental plots of Banaras Hindu University, Varanasi receiving different levels of nitrogen treatment. The superscript letters a, b and c indicate the presence of the species in control, 6 and $12 \text{ g N m}^{-2} \text{ year}^{-1}$ treated plots respectively. Other superscript letters are trait initials; H, Perennial; I, Annual; J, Biennial; K, Forb; L, Grass; M, Legume; N, Sedge; O, Large; P, Medium; Q, Small

Biomass (gm^{-2})	Species	Family
7.72	<i>Digitaria sanguinalis</i> L. ^{a,b,c,I,L,O}	Poaceae
7.47	<i>Oplismenus burmannii</i> Retz. ^{a,b,c,I,L,Q}	Poaceae
5.96	<i>Clerodendrum indicum</i> L. ^{a,b,c,H,K,O}	Verbenaceae
4.82	<i>Commelina benghalensis</i> L. ^{a,b,c,I,K,Q}	Commelinaceae
4.71	<i>Dichanthium annulatum</i> Forsk. ^{a,b,c,H,L,O}	Poaceae
3.74	<i>Commelina nudiflora</i> L. ^{a,b,I,K,Q}	Commelinaceae
3.67	<i>Parthenium hysterophorus</i> L. ^{b,c,I,K,O}	Asteraceae
3.56	<i>Achyranthes aspera</i> L. ^{a,b,c,H,K,O}	Amaranthaceae
3.34	<i>Convolvulus pluricaulis</i> Choisy. ^{a,b,H,K,Q}	Convolvulaceae
3.33	<i>Panicum psilopodium</i> Trin. ^{a,b,c,I,L,O}	Poaceae
3.31	<i>Ageratum conyzoides</i> L. ^{a,b,c,I,K,P}	Asteraceae
3.05	<i>Hyptis suaveolens</i> Poir. ^{b,c,H,K,O}	Lamiaceae
2.54	<i>Cayratia trifolia</i> L. ^{a,b,c,J,K,O}	Vitaceae
2.42	<i>Malvastrum tricuspidatum</i> L. ^{a,b,c,H,K,Q}	Malvaceae
2.37	<i>Herpestis monniera</i> Kunth. ^{a,b,c,H,K,Q}	Scrophulariaceae
2.32	<i>Atylosia marmorata</i> Benth. ^{a,b,H,M,O}	Fabaceae
2.32	<i>Anisomeles ovata</i> R. Br. ^{a,b,I,K,O}	Lamiaceae
1.93	<i>Amaranthus spinosus</i> L. ^{b,c,I,K,Q}	Amaranthaceae
1.88	<i>Blepharis repens</i> Vahl. ^{a,b,c,H,K,O}	Acanthaceae
1.81	<i>Alternanthera sessilis</i> L. ^{b,c,H,K,P}	Amaranthaceae
1.78	<i>Cynodon dactylon</i> Pers. ^{a,b,H,L,P}	Poaceae
1.69	<i>Anagallis arvensis</i> L. ^{b,c,I,K,Q}	Primulaceae
1.62	<i>Cyperus kyllingia</i> Endl. ^{a,b,c,I,N,Q}	Cyperaceae
1.39	<i>Argemone mexicana</i> L. ^{b,c,I,K,P}	Papaveraceae
1.37	<i>Desmodium gangeticum</i> L. ^{a,b,c,H,M,O}	Fabaceae
1.26	<i>Eulaliopsis binata</i> Retz. ^{a,b,c,H,L,O}	Poaceae
1.26	<i>Urena lobata</i> L. ^{b,c,H,K,P}	Malvaceae
1.18	<i>Euphorbia pulcherrima</i> Willd. ^{b,c,H,K,O}	Euphorbiaceae
1.14	<i>Cissampelos pareira</i> L. ^{a,b,H,K,O}	Menispermaceae
1.08	<i>Portulaca oleracea</i> L. ^{b,c,I,K,Q}	Portulacaceae
1.02	<i>Euphorbia thamifolia</i> L. ^{b,c,I,K,Q}	Euphorbiaceae
1.01	<i>Croton bonplandianum</i> Bail. ^{a,b,c,H,K,P}	Euphorbiaceae
0.98	<i>Eleusine indica</i> Gaertn. ^{a,b,I,L,O}	Poaceae
0.84	<i>Eragrostis tenella</i> L. ^{b,c,I,L,P}	Poaceae
0.79	<i>Sonchus oleraceus</i> L. ^{b,c,I,K,O}	Asteraceae
0.73	<i>Cyperus rotundus</i> L. ^{a,b,I,N,P}	Cyperaceae
0.69	<i>Scoparia dulcis</i> L. ^{a,b,H,K,Q}	Scrophulariaceae
0.65	<i>Corchorus olitorius</i> L. ^{a,b,c,I,K,O}	Malvaceae
0.61	<i>Tridax procumbens</i> L. ^{a,b,H,K,Q}	Asteraceae
0.56	<i>Coccinia cordifolia</i> L. ^{a,b,H,K,O}	Cucurbitaceae
0.49	<i>Nicotiana plumbaginifolia</i> Viv. ^{b,c,I,K,P}	Solanaceae
0.43	<i>Ammannia baccifera</i> L. ^{b,I,K,P}	Lythraceae
0.35	<i>Oldenlandia ambellata</i> L. ^{b,H,K,Q}	Rubiaceae
0.33	<i>Oxalis corniculata</i> L. ^{b,H,K,P}	Oxalidaceae
0.29	<i>Ruellia tuberosa</i> L. ^{b,H,K,P}	Acanthaceae
0.26	<i>Euphorbia hirta</i> L. ^{a,b,c,H,K,Q}	Euphorbiaceae
0.26	<i>Corchorus tridens</i> L. ^{a,b,c,H,K,O}	Malvaceae
0.20	<i>Cyperus fuscus</i> L. ^{b,I,N,Q}	Cyperaceae
0.16	<i>Desmodium triflorum</i> L. ^{b,H,M,Q}	Fabaceae

Figure 1 reveals that when species richness, evenness and Shannon indices are used as diversity parameters to relate with productivity at relatively smaller area (at 15 m²); the fitness of *D–P* relationship is equally good in all the cases ($R^2 = 0.85–0.95$), while at relatively larger area (45 m²); the Shannon index shows greater correlation coefficient ($R^2 = 0.86$) than other measures of diversity ($R^2 = 0.38$ for richness and 0.35 for evenness).

Grace³³ surveyed the literature on *D–P* relationship in herbaceous plant communities and concluded that most studies relating plant species richness to plant biomass in small plots exhibited a hump-shaped relationship. Additionally, Grace *et al.*³⁴ reported that the influence of small-scale species richness on productivity could be weak. Similarly, Adler *et al.*⁶ addressed this problem by establishing standardized methodology in 48 herbaceous-dominated communities on five continents. Their study revealed that fine-scale species richness could not be a good predictor of productivity, neither within sites/regions nor across the globe.

Based on the above results, we conclude that depending on the area under investigation and differences in N supply, the species diversity may increase, decrease or produce hump-shaped pattern against the primary productivity because these patterns are driven by the plant functional group composition rather than changes in biodiversity *per se* at different N-enrichment levels.

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ACKNOWLEDGEMENTS. We thank DST, New Delhi, for financial support. We also thank to Dr Forest Isbell (Department of Plant Biology, University of Georgia, Athens) and Dr Gyan P. Sharma (Department of Environmental Biology, University of Delhi) for useful comments that helped improve the manuscript.

Received 22 June 2014; revised accepted 12 March 2015

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